HOST SPECIFICITY AND DISTRIBUTION OF THE KLEPTOBIOTIC SPIDER *ARGYRODES ANTIPODIANUS* (ARANEAE, THERIDIIDAE) ON ORB WEBS IN QUEENSLAND, AUSTRALIA

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ABSTRACT. We investigated host specificity, the effects of host size, and the effects of the size, structure and occupancy of host webs on the abundance of the kleptobiotic spider *Argyrodes antipodianus* O.P.-Cambridge 1880. The kleptobiont is not host specific, but does prefer orb webs that are surrounded by a scaffold of threads (barrier-web). Across all hosts, host size had little effect on the abundance of the kleptobiont, while host density and the presence of other species of *Argyrodes* on webs had no effect. Web diameter, although not strongly related to the abundance of *A. antipodianus* in the field, limited kleptobiont numbers in greenhouse experiments. On webs of the Golden Orb Spider, *Nephila plumipes* (Latreille 1804), numbers of *A. antipodianus* were not affected by size of the scaffold or by aggregation of host webs. However, presence of host males was associated with a significantly higher abundance of *A. antipodianus*, suggesting that these kleptoparasites may take advantage of distracted females and impose a cost on mating in *N. plumipes*.

Many spiders of the genus *Argyrodes* Simon 1864 live in close association with web-building spiders, and remove and feed on prey items captured in the webs of their hosts. These small web visitors are referred to as "kleptoparasites" or "kleptobionts" (Vollrath 1984, 1987; Elgar 1993). Although observations of their unusual foraging behavior are relatively common, little is known of the mechanisms that influence the infestation levels of kleptobiotic *Argyrodes* on host webs. Abundance and diversity of *Argyrodes* on webs may vary considerably among and within host species (Kaston 1965; Levi 1978, 1985; Whitehouse 1988; Elgar 1989), with up to 46 individuals and up to 3 species found on a single web (Exline & Levi 1962; Vollrath 1981).

The abundance of these kleptobionts may be influenced by a range of factors such as prey availability, weather, host behavior or web characteristics (Robinson & Robinson 1973; Smith-Trail 1981; Vollrath 1984; Larcher & Wise 1985; Vollrath 1987; Whitehouse 1988; Elgar 1989; Cangialosi 1990a, b; Whitehouse & Jackson 1993; Elgar 1993). Influential web characteristics could include size, architecture (e.g., relative size of web scaffold), abundance or aggregation of host

webs (Whitehouse 1988; Elgar 1993). Interactions with the host or other web "visitors," such as host males or other kleptobionts also could influence web colonization (Vollrath 1984, 1987; Grostal & Walter 1997).

Argyrodes antipodianus O.P.-Cambridge 1880 is an abundant kleptobiont on the webs of orb weaving spiders in southeast Queensland. This spider is a relatively small-bodied species (*ca.* 3 mm long), that is easily recognized in Australia by its conical, bright silver abdomen (Grostal, in press). *Argyrodes antipodianus* is associated with at least ten host species that build four different types of web (orb, funnel, tangle and space), but in New Zealand the kleptobiont is most common on the non-cribellate, sticky orb webs of *Eriophora pustulosa* (Walckenaer 1841) (Whitehouse 1988; Elgar 1993). Consequently, Whitehouse (1988) refers to *A. antipodianus* as a host specialist (*sensu* Vollrath 1984).

In this paper we used field surveys to examine the host range of *A. antipodianus*, and to investigate how the abundance of this spider is influenced by the architecture, size and relative abundance of host webs, and presence of other species of *Argyrodes* on these webs. We then examined *A. antipodianus* on webs of one of its common hosts, the Golden Orb
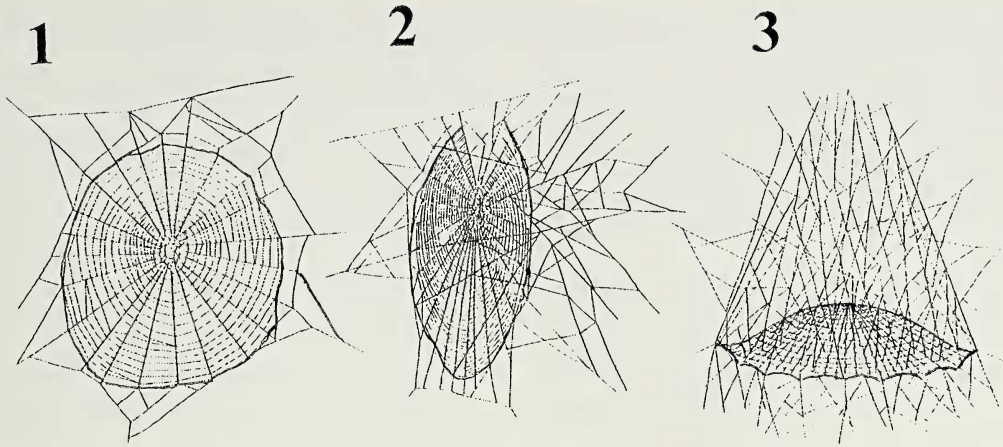
Figures 1–3.—Three types of orb web sampled during four surveys in eastern Queensland: 1. Orb only (e.g., *Eriophora transmarina*), frontal aspect; 2. Orb and barrier (e.g., *Nephila plumipes*), fronto-lateral aspect; 3. Orb and tangle (e.g., *Cyrtophora moluccensis*), lateral aspect.

Spider, *Nephila plumipes* (Latreille 1804) and determined the influence of the relative size of barrier-web, web aggregation and the number of host males on kleptobiont numbers. Finally, we used greenhouse experiments to establish the effect of orb size of *N. plumipes* on the retention of *A. antipodianus* on webs. We predicted that the kleptobionts would be positively associated with web size and web aggregation, but negatively associated with numbers of other kleptobionts and of host males.

METHODS

Host range and abundance of *A. antipodianus*.—We conducted four surveys during 1995 in eastern Queensland: two surveys in the south east (Pinkenba 27°25'S, 153°07'E and Everton Park, Brisbane, 27°25'S, 152°59'E), one on the central coast (Yeppoon, 23°07'S, 150°44'E) and one in the far north (Cairns 16°53'S, 145°45'E). The Everton Park site (area = 2500 m²) was surveyed during October and was dominated by a semi-closed dry sclerophyll forest. Pinkenba (area = 16,000 m²), surveyed in August, consisted of an open stand of casuarina. The site at Yeppoon (area = 12,000 m²) was censussed in May and consisted of an open palm forest, while the one in Cairns (area = 3,920 m²) was a closed rainforest thicket, and was examined in August. The month and location of the surveys depended on the opportunity to visit the sites.

We searched each site for orb webs that were located up to 200 cm above ground level and were over 9 cm in diameter. Spiders that constructed smaller webs were often juvenile and thus difficult to identify. For each web we collected the following data: species of the web builder, the spider's body length (cephalothorax and abdomen, measured with a clear ruler to nearest mm), the diameter of the orb (to nearest cm), and the number and species of *Argyrodes* on the web. The webs were divided into three categories based on their architecture: orb only, orb with barrier, and orb with tangle (Fig. 1). A barrier is a three-dimensional scaffold of non-sticky threads in front of and behind an orb (Fig. 2). A tangle consisted of a dense tent-like scaffold (Fig. 3) that extended above and below the orb. Tangles were more complex and larger relative to orb size, than barriers. All *Argyrodes* species were collected and preserved in 80% ethanol for later identification. A sample collection of the spiders was deposited with the Queensland Museum (Brisbane, Australia).

Abundance of *A. antipodianus* on webs of *N. plumipes*.—We conducted two additional surveys on separate plots at Pinkenba (one during April, the other during May 1995). In the first survey we sampled the webs of adult *N. plumipes* only, and in the second survey we examined webs of all stages of *N. plumipes*. The plots were adjacent to the one previously sampled for a range of different hosts

(see above) and consisted of an open stand of casuarina. For both surveys, we searched each site for webs of *N. plumipes* up to a height of 2.5 m, using a stepladder for webs above 2 m. All data were collected as in the previous surveys, except that we used carapace width to measure host size (a more precise measure at the intraspecific level; Higgins & Rankin 1996).

Additionally, we recorded the presence of visiting host males on webs and we qualitatively assigned the webs into five categories, based the complexity of the barrier (0 = no barrier; 4 = most complex barrier). We categorized barrier complexity by visually comparing the size of the orb relative to the volume occupied by the barrier threads and their density (no. of threads/volume). To check the accuracy of this estimation, we collected 10 clean webs for each of the categories 1 to 4 (webs with barriers present). We used dissecting scissors to separate orbs from barriers during collection. Then, for each web, we cleaned the silk from any debris and separately weighed orbs and barriers with an electronic balance in the laboratory. We used these results to calculate the mean ratio ($\pm$ SE) of barrier weight : orb weight for each category and to check if the categories are discrete (i.e., if the means significantly differ).

Finally, for the survey of adult *N. plumipes* we recorded whether host webs were aggregated or not. A web was ranked as aggregated if its threads overlapped or interlocked with those of another web (Elgar 1989). Aggregations containing webs of immature hosts were excluded from the sample.

Retention of *A. antipodianus* on webs of *N. plumipes*.—The experiments were conducted in a ventilated greenhouse (Brisbane, September 1995). We used female *N. plumipes* of two age groups: juveniles (10–11 mm long) and adults (27–32 mm long), but only adult females of *A. antipodianus*. The spiders were housed in large cages (170 $\times$ 170 $\times$ 170 cm) which were covered with a fine plastic mesh. Four wooden racks, composed of a central rod (165 cm high) with four arms, were placed in the corners of each cage to provide support for webs spun by host spiders (Grostal & Walter 1997). Eight cages were used for each experiment, which was repeated six times over 18 days. One *N. plumipes* was

placed in each cage 48 hours before each trial and allowed to spin a web.

Four adult and four juvenile *N. plumipes* were used for each experiment. First, we randomly removed four hosts (two juveniles and two adults) from their webs. Care was taken not to damage the web while removing the spiders. Thus, each test consisted of four webs of adult *N. plumipes*: two with hosts included and two with hosts removed, and four webs of juveniles: two with hosts present, and two with hosts removed. Ten *A. antipodianus* were then placed on each web. After 24 h we recorded the number of *A. antipodianus* that remained on the webs.

Statistical analysis.—For surveys of host range and abundance of *A. antipodianus*, we used linear regression to estimate the relationship of the number of *A. antipodianus* per web with: 1) host body length; and 2) diameter of host web. The effect of presence of other *Argyrodes* species ($+/-$) on webs on the mean number of *A. antipodianus* per web was analyzed using single-factor ANOVA. Prior to the analysis, data were log-transformed for normality. Data from all four sites were pooled for the above analyses. Finally, we calculated the mean number of *A. antipodianus* per web for each host species, on every site ($n = 27$). Then, we regressed these means against the density of the corresponding host species at a given site (no. individuals/10,000 m^2, see Table 1). We examined all regression data with scatterplots to check for non-linear relationships.

For surveys of *N. plumipes*, we regressed the number of *A. antipodianus* per web against width of host carapace and diameter of host web. The effects of: 1) aggregation of host webs ($+/-$); 2) presence of male *N. plumipes* ($+/-$); and 3) the rank of web barrier (0, 1, 2, 3, 4) on the abundance of *A. antipodianus* (number per web) were analyzed separately with single-factor ANOVA. For the greenhouse experiments, we compared the numbers of *A. antipodianus* retained on webs that were spun by juvenile and adult *N. plumipes*, with and without the hosts, using a two-way ANOVA. All data were normalized by log-transformation before analysis.

RESULTS

Host range and abundance of *A. antipodianus*.—A total of 744 webs was examined

Table 1.—Average body length (mm) of host spiders (cephalothorax + abdomen), density (no./10,000 m²) of host webs sampled and the average number of *Argyrodes antipodianus* on three types of host web (orb only, orb and barrier, orb and tangle) at four sites in coastal Queensland: Everton Park, Pinkenba (both in south-east), Yeppoon (central-east) and Cairns (far north). Values are totals or means ± standard errors.

Site/Web type/Host	Host length (No. webs/10,000 m²)	*A. antipodianus* per web
Everton Park		
Orb only		
Araneus dimidiatus	7.7 ± 1.0 (156)	0.2 ± 0.1
Argiope sp.	6.9 ± 2.3 (16)	0
Eriophora transmarina	12.7 ± 2.1 (24)	0.3 ± 0.2
Leucauge sp.	6.7 ± 1.4 (36)	0
Orb & Barrier		
Nephila plumipes	12.9 ± 4.1 (292)	2.7 ± 0.3
Orb & Tangle		
Cyrtophora hirta L. Koch 1872	6.0 (4)	0
Cyrtophora moluccensis (Doleschall 1857)	10.9 ± 4.1 (84)	0.2 ± 0.2
Pinkenba		
Orb only		
Araneus eburnus	4.0 ± 0.7 (1)	0
Argiope sp.	5.5 (1)	1.0
Eriophora transmarina	4.9 ± 0.9 (68)	0.02 ± 0.01
Leucauge sp.	5.9 ± 1.2 (22)	0
Orb & Barrier		
Nephila plumipes	10.7 ± 3.6 (116)	5.9 ± 0.3
Orb & Tangle		
Cyrtophora hirta	4.0 ± 2.1 (3)	2.0 ± 1.7
Cyrtophora moluccensis	8.3 ± 4.1 (5)	6.0 ± 1.7
Yeppoon		
Orb only		
Araneus dimidiatus	5.4 ± 1.1 (36)	0.1 ± 0.1
Gasteracantha sp.	4.3 ± 0.9 (10)	0
Orb & Barrier		
Nephila pilipes (Fabricius 1793)	21.3 ± 11.5 (7)	0.6 ± 0.4
Nephila plumipes	16.5 (1)	0
Orb & Tangle		
Cyrtophora sp.	6.3 ± 1.2 (8)	0
Cairns		
Orb only		
Araneus dimidiatus	4.9 ± 0.8 (311)	0.2 ± 0.1
Argiope sp.	10.7 ± 2.9 (33)	0.3 ± 0.2
Eriophora transmarina	4.4 ± 0.5 (13)	0
Gasteracantha sp.	5.9 ± 1.8 (20)	0
Leucauge sp.	4.8 ± 1.2 (20)	0
Orb & Barrier		
Nephila pilipes	12.8 ± 10.9 (20)	0.4 ± 0.3
Nephilengys sp.	5.6 ± 1.8 (13)	0
Orb & Tangle		
Cyrtophora sp.	10.0 ± 2.8 (5)	3.5 ± 1.5

Table 2.—Average number of individuals of each species of *Argyrodes* per web ($\pm$ standard error) at Everton park (south-east Queensland), Pinkenba (south-east Queensland), Yeppoon (central-east Queensland) and Cairns (far north Queensland).

Species	Everton Park	Pinkenba	Yeppoon	Cairns
A. antipodianus	1.40 ± 0.19	3.36 ± 0.24	0.12 ± 0.05	0.19 ± 0.05
A. rainbowi	0.13 ± 0.04	0.03 ± 0.01	—	—
A. species 1	0.22 ± 0.07	0.03 ± 0.01	0.01 ± 0.01	—
A. fissifrons	0.09 ± 0.04	—	—	—
A. miniaceus	—	—	0.22 ± 0.12	0.25 ± 0.08
A. kulczynski	—	—	0.24 ± 0.08	0.01 ± 0.01

in the four surveys, and *A. antipodianus* was associated with eight of the 12 host species sampled (Table 1). Only webs of *Araneus eburnus* (Keyserling 1886), *Gasteracantha* sp., *Leucauge* sp. and *Nephilengys* sp. had no *A. antipodianus*; however, for some of these hosts (e.g., *Nephilengys* sp.) very few webs were found (Table 1). Webs of *Araneus dimidiatus* (L. Koch 1871), present at every site except Pinkenba, consistently had low numbers of *A. antipodianus*, in spite of the high abundance of this host species (Table 1). Similarly, webs of *Eriophora transmarina* (Keyserling 1865), although relatively common in the southeastern Queensland sites, had very few *A. antipodianus* (Table 1). There was no apparent linear relationship between density of hosts (no. per 10,000 m²) and the mean number of *A. antipodianus* per web across all four sites ($R^2 = 0.02$; $F_{1, 25} = 0.53$, $P = 0.47$), although spiders belonging to *Nephila* spp. and *Cyrtophora* spp., were clearly the preferred hosts (Table 1).

At Everton Park and Pinkenba, *A. antipodianus* was over six times more abundant than any other species of *Argyrodes*; however, in tropical Queensland (Cairns and Yeppoon) other species of *Argyrodes* were more abundant (Table 2). In Cairns, *A. miniaceus* (Doleschall 1857) was more numerous, while Yeppoon was dominated by *A. miniaceus* and *A. kulczynski* (Roewer 1942). Three additional species of *Argyrodes* (*A. fissifrons* O.P.-Cambridge 1869, *A. rainbowi* (Roewer 1942) and *Argyrodes* sp. 1) were also collected. In the presence of other species of *Argyrodes*, the abundance of *A. antipodianus* (2.6 ± 0.5 spiders per web) was somewhat higher than that on webs with no congeners, although the difference was not significant (1.8 ± 0.1 spiders per web; ANOVA: $F_{1, 745} = 2.83$, $P = 0.093$).

Both body length and orb diameter of host spiders showed a positive linear relationship with the numbers of *A. antipodianus*. When data from all surveys were pooled, host length accounted for 28% of the variance in *A. antipodianus* numbers ($F_{1, 742} = 286.5$, $P < 0.0001$). Orb diameter seemed to impose an upper limit on the numbers of the kleptobiont (Fig. 4: broken line), although the two variables were not strongly related ($R^2 = 0.13$; $F_{1, 745} = 107.3$, $P < 0.0001$). Orb diameter also showed a positive relationship with the body length of hosts ($R^2 = 0.60$; $F_{1, 742} = 1118.6$, $P < 0.0001$).

Species of *Nephila* and *Nephilengys* construct webs that consist of a vertical orb and a non-viscid barrier (Fig. 2). *Cyrtophora* spp. make non-viscid, horizontal orbs with an extensive tangle (Levi 1978; Shear 1994; Fig. 3). Spiders that construct webs consisting almost exclusively of a catching orb with little or no barrier include *Araneus dimidiatus*, *A. eburnus*, *Argiope* sp., *Eriophora transmarina*, *Gasteracantha* sp. and *Leucauge* sp..

Architecture of host webs (Fig. 1) influenced the abundance of *A. antipodianus* (ANOVA: $F_{1, 745} = 217.04$, $P < 0.0001$). When all data were pooled, webs containing orbs with barriers had the highest numbers of the kleptobiont (mean of 4.6 ± 0.3/web). Generally, orbs with a tangle had intermediate numbers of *A. antipodianus* (1.5 ± 0.5/web) and webs that consisted only of orbs had the lowest numbers (0.09 ± 0.02/web). In Cairns webs with orb and tangle had the most *A. antipodianus*, although these results applied only to two individuals of an unidentified species of *Cyrtophora*.

Abundance of *A. antipodianus* on webs of *N. plumipes*.—At Pinkenba we examined a total of 299 webs in the survey of all stages
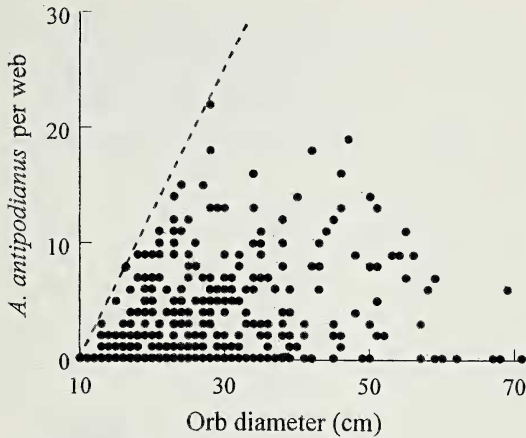
Figure 4.—Numbers of *Argyrodes antipodianus* per web against orb diameter (cm) of host webs at Everton Park, Pinkenba, Yeppoon and Cairns.

of *N. plumipes* and 213 webs in the survey of adult *N. plumipes*. There was an average of 5.7 ± 0.3 *A. antipodianus* per web in the former and 2.3 ± 0.1 in the latter census. Numbers of *A. antipodianus* were positively related with the width of host carapace, although, as in the across-species comparison, this relationship was not strong for all host stages (R^2 = 0.27; $F_{1, 297}$ = 109.7, $P < 0.0001$) or adult hosts (R^2 = 0.15; $F_{1, 211}$ = 36.18, $P < 0.0001$). Orb diameter of *N. plumipes* showed a similar pattern of relation with the abundance of *A. antipodianus* (all hosts R^2 = 0.22, $F_{1, 297}$ = 85.95, $P < 0.0001$; adult hosts R^2 = 0.12, $F_{1, 211}$ = 28.44, $P < 0.0001$).

Our visual estimation of the complexity of the barrier (categories 0 to 4) was sufficiently accurate, since the ratios of orb weight/barrier weight (± SE, n = 10) differed between categories (category 1 = 0.1 ± 0.02; 2 = 0.3 ± 0.1; 3 = 1.1 ± 0.4; 4 = 1.9 ± 0.5). Nevertheless, barrier complexity did not have an effect on *A. antipodianus* in either survey (AN-OVA, all webs $F_{4, 289}$ = 1.44, P = 0.221; adults only $F_{3, 209}$ = 0.36, P = 0.786).

Aggregation (±, recorded only for adult webs) did not affect the numbers of *A. antipodianus* (ANOVA, $F_{1, 211}$ = 2.13, P = 0.146). However, abundance of these kleptobionts was over 65% higher on webs that had male *N. plumipes*. This result was highly significant for the survey of all stages of *N. plumipes*, with 9.0 ± 1.0 *A. antipodianus* on webs with males (n = 24), and 5.5 ± 0.3 kleptobionts on webs without males (n = 275; ANOVA: $F_{1, 297}$ = 15.78, $P < 0.001$) and for the census of adult hosts (Fig. 5; ANOVA: $F_{1, 211}$ = 7.96, P = 0.005).

Retention of *A. antipodianus* on webs of *N. plumipes*.—On average, after 24 hours, large webs (32 ± 4 cm diameter) built by adult *N. plumipes* retained over 85% more *A. antipodianus* than small webs (18 ± 3 cm diameter), built by juvenile hosts (ANOVA, $P < 0.0001$; Fig. 6, Table 3). However, the presence of hosts on webs was of no consequence to the kleptobiont (ANOVA, P = 0.895; Table 3). When juvenile hosts were excluded, six of the twelve webs were destroyed or damaged by more than 30% by *A. antipodianus* (pers. obs.), and were not included in the analysis. Webs of adult *N. plumipes* did not differ in shape or architecture from those built by the juveniles.

DISCUSSION

Kleptobiotic *Argyrodes* may be found on a range of webs (Kaston 1965; Elgar 1993), although they are likely to be more abundant on webs that are easy to forage on, supply sufficient food and provide ample refuge. Whitehouse (1988) found that in New Zealand *A. antipodianus* specialized on a single host species, *Eriophora pustulosa*, in whose webs it foraged most efficiently. We have unpublished data that is consistent with Whitehouse

Table 3.—Two-way ANOVA for the effect of web size and presence of *N. plumipes* on the numbers of *A. antipodianus* retained on webs after 24 hours in the greenhouse (initial number of kleptobionts per web = 10).

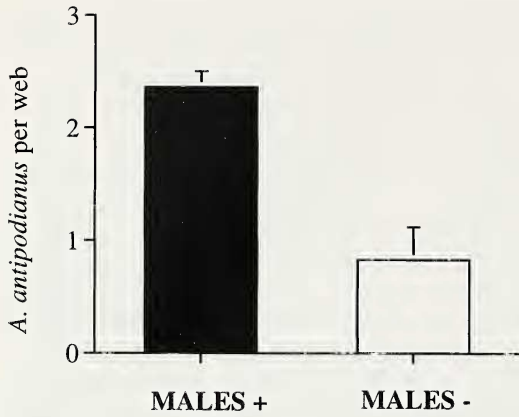| Category	df	MS	F	P
Web size	1	0.903	51.00	<0.0001
Host presence	1	0.0003	0.02	0.895
Web size * host pres.	1	0.021	1.19	0.282
Residual	38	0.02		

Figure 5.—Average number of *Argydoes antipodianus* per web on webs of adult *Nephila plumipes* females that included (males +), or did not include male hosts (males −).
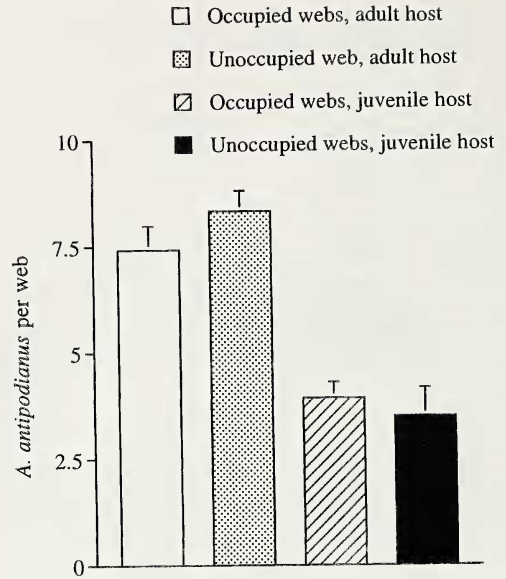

Figure 6.—Effects of web size and host presence on the retention of *Argyrodes antipodianus* (number remaining after 24 hours) on webs of *Nephila plumipes* in the greenhouse. Data presented as means + standard error.

(1988), i.e., other webs such as tangle webs constructed by theridiids (e.g., *Latrodectus* spp.) or space webs made by amaurobids (e.g., *Badumna* spp.) were rarely colonized by *A. antipodianus* (P.G., pers. obs.). However, we also found that the kleptobiont has a broad host distribution, perhaps because our sampling areas had a higher diversity of web spiders than those examined by Whitehouse (Elgar 1993). Additionally, we found some evidence of web specificity by this kleptobiont, as it was found primarily on orb webs that included a scaffold (barrier or tangle): those of *Nephila* and *Cyrtophora* species.

Elgar (1993) pointed out that host specificity is likely to vary continuously and can be influenced by the abundance and diversity of hosts. Our data show that relative abundance of webs of each host species was not significantly correlated with the abundance of *A. antipodianus*. However, availability of hosts probably does affect host choice by the kleptobiont. For example, *Eriophora pustulosa* were the preferred hosts in New Zealand during summer (Whitehouse 1988), but these were the only orb weavers present in the study site. On the other hand, in the presence of more complex orb webs (with scaffold) in Queensland, orb weavers that construct simple orb webs similar to *E. pustulosa* had few or no *A. antipodianus*.

If kleptobiotic *Argyrodes* have a negative effect on their hosts, then web characteristics that favor them will carry a disadvantage to the web owner and may be under conflicting selective pressures (e.g., larger webs might catch more food, but may also increase the kleptobiont load). Elgar (1989) found that the intensity of infestation of *Nephila edulis* (Labillardiere 1799) webs by *A. antipodianus* was correlated with host size. Our data show a positive correlation between the number of these kleptobionts and both host size and orb diameter, although little of the variance is explained (13–28%). This may be because host size or orb diameter is not always clear indicators of web size for spiders that construct webs of varying architecture. For instance, while orbs built by *Cyrtophora* (orb & tangle) are small, those of *Nephila* (orb & barrier) are large relative to total web space (Figs. 2, 3). Further, our results could have been confounded by survey site, season and species of host, which were all pooled. However, the correlation did not improve when we controlled for variation in web architecture, site and host species by using only *N. plumipes*. Nevertheless, orb size may impose an upper limit on the numbers of *A. antipodianus* on host webs: large orbs may accommodate few or many *A. antipodianus*, but small orbs contain only few kleptobionts. This was supported by our data

from the greenhouse, which showed that independent of host presence, small webs (juvenile *N. plumipes*) retain fewer *A. antipodianus* than large webs (adult hosts).

Although we examined 512 webs in our surveys of *N. plumipes*, we did not find an obvious effect of web architecture or aggregation on the numbers of *A. antipodianus*; and perhaps the distribution of this kleptobiont is more random than previously hypothesized (Elgar 1989). However, apart from the structural characteristics of webs that we measured, several other factors may directly influence the number of *A. antipodianus* on webs. These could include the web tenacity of hosts (Levi 1978), food abundance and quality, host behavior and environmental factors, all of which ought to be examined in future studies.

Contrary to our hypothesis that other web visitors might have a damping effect on numbers of *A. antipodianus*, the presence of other *Argyrodes* had no significant effect. Also, surprisingly, male hosts were associated with greatly elevated numbers of this kleptobiont, as there were two-thirds more *A. antipodianus* on webs of female *N. plumipes* colonized by males, than on webs with no males. We offer two alternative hypotheses to explain this unexpected result. First, both males and kleptobionts may be responding to the same factors, e.g., food availability, position in wind corridors or insolation. Also, pheromones emitted by female hosts can be perceived not only by the males, but perhaps also by the kleptobionts, consequently facilitating web location. Second, the activity of *Nephila* males (including feeding and mating attempts) may be beneficial to *A. antipodianus* through disturbance of the web and distraction of the female host. Thus, with males present, *A. antipodianus* would face lower levels of aggressive response by the web owner, and perhaps have a higher foraging success, thus remaining on the web longer. Possibly, *A. antipodianus* engages in "smokescreening" behavior (Wilcox et al. 1996) by increasing its feeding while female hosts are distracted. If mating attempts of male *N. plumipes* cause higher infestation levels of kleptobionts, then reproduction of this host may come at a previously unnoticed cost.

ACKNOWLEDGMENTS

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